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The “neutral” community structure of planktonic herbivores, tintinnid ciliates of the microzooplankton, across the SE Tropical Pacific Ocean

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Abstract

Across a species-rich area, the SE Pacific Ocean, the community characteristics of a group of planktonic herbivores was assessed. A series of 22 stations between the Mar-
5 quise Islands (7° S 142° W) and the coast of Chile (35° S 73° W) was sampled during the BIOSOPE cruise in 2004. The relationships between taxonomic diversity, morphological diversity, patterns of tintinnid species assemblage, and phytoplankton abundance were examined. Tintinnid community characteristics were estimated from large volume (20–60 l) discrete depth sampling and phytoplankton were characterized based on
10 HPLC pigment signatures. Across the transect, average water column concentrations of tintinnids ranged from 2–40 cells l⁻¹ or 8–40 ng C l⁻¹, and were positively related to chlorophyll a concentrations which varied between 0.07–2 µg l⁻¹. Large numbers of tintinnid taxa were found, 18–41 species per station, yielding a total of 149 species. Among stations, morphological and taxonomic diversity metrics co-varied but were not significantly related to phytoplankton diversity estimated using a pigment-based
15 size-diversity metric. Taxonomic diversity of tintinnids, as H' or Fishers' alpha, was inversely related to chlorophyll concentration and positively to the depth of the chlorophyll maximum layer. For each station, species abundance distributions were compared to geometric, log-series and log-normal distributions. For most stations, the observed distribution most closely matched log-series, coherent with the neutral theory of random
20 colonization from a large species pool. Occurrence rates of species were correlated with average abundance rather than specific characteristics of biomass or lorica oral diameter (mouth) size. Among stations, species richness was correlated with both the variety of mouth sizes (lorica oral diameters) as well as numbers of species per mouth size, also consistent with random colonization.

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1 Introduction

Oceanographic and biological surveys in the early 20th century identified the SE Pacific as extraordinarily species-rich (e.g., the Agassiz Expedition of 1904–1905 and the Carnegie Expedition of 1928–1929). With the decline of survey campaigns, the zone was very rarely sampled (Hasle, 1959) and in common with other oceanic areas, modern research efforts and major programs (such as Eastropac in the late 1960s), have been process studies focusing on parameters such as biomass estimates and rate measures of primary and secondary production. Interestingly, from these system studies a paradigm has emerged stressing the apparent efficiency of tropical and subtropical food webs. Algal biomass is low, often lower than one might expect given concentrations of nutrients (i.e., zones of high nutrient low chlorophyll, HNLC) and nearly all the primary production is consumed. The efficiency of grazers, especially protists, has often been invoked as an explanation, at least partial (Leising et al., 2003) for the maintenance of low algal biomasses. The diversity of tropical and subtropical pelagic systems may be related to the efficiency of both primary producers and secondary consumers. However, the existence or importance of the link between trophic efficiency and diversity in planktonic communities is difficult to evaluate because community characteristics have received very little attention, especially with regard to the primary consumers, the microzooplankton. These grazers have long been identified as the likely dominant consumers of algal production, given their relatively high biomass compared to metazoan grazers, especially in systems such as the SE Pacific (Beers and Stewart, 1971). Here we focus on large-scale geographic patterns across the SE Pacific Ocean for a particular group of these organisms members of the ciliate order Tintinninoidea, tintinnid ciliates of the microzooplankton, which are united ecologically as grazers on pico and nanplankton.

Tintinnid ciliates are characterized by the possession of a tube or vase-shaped shell or lorica into which the ciliate cell can contract. They are generally a minority among the microzooplankton, representing 5–10% of ciliate numbers (e.g., Dolan and Marassé,

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1995) but occasionally dominate the microzooplankton (Karayanni et al., 2005). Tintinnids, as loricate choreotrich ciliates, are considered a monophyletic group in traditional ciliate classification schemes and based on results of recent molecular work (e.g., Agatha et al., 2004). The group is species-rich with over 700 species distinguished in the monographs of Kofoed and Campbell (1929, 1939).

Similar to foraminifera and radiolarians, species descriptions have been based on skeletal architecture. However, species in some genera are known to be polymorphic (e.g. Laval-Peuto, 1983; Williams et al., 1994). Characteristics of the lorica are not only of taxonomic but also ecological significance. The diameter of the mouth end of the lorica, the lorica oral diameter (LOD), is related to the size of the food items ingested by the ciliate. Hienbokel (1978) noted that the largest prey ingested were about half the LOD and Dolan et al. (2002) found that tintinnid feeding rates were maximal on prey sizes equal to about 25% of LOD. Thus, in tintinnid ciliates the lorica distinguishes species both taxonomically and ecologically. Not surprisingly then, morphological diversity, in terms of LOD sizes, and taxonomic diversity co-vary both spatially and temporally.

Between the Moroccan upwelling system and the Eastern Mediterranean, taxonomic and morphological diversity of tintinnids showed parallel trends (Dolan et al., 2002). Diversity increased from the upwelling area into the Western Mediterranean and declined slightly towards the oligotrophic Eastern Mediterranean. Both taxonomic and morphological (LOD) diversity were correlated with a chlorophyll size-diversity estimate. In temperate systems, seasonal changes in the average LOD of tintinnid communities are well-known (e.g., Verity, 1984.) In a recent study of the seasonal changes in a tropical lagoon, median LOD of the tintinnid community shifted with the fraction of chlorophyll a >10 μm (Dolan et al., 2006). The numbers of species were relatable to numbers of LOD size-classes and taxonomic diversity was correlated with LOD size-class diversity.

Here we examine patterns of community assembly across the SE Pacific. The areas sampled included zones with highest recorded species richness of tintinnids (>100 spp, at reported for some stations in Kofoed and Campbell, 1939) and the clearest waters of

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the world ocean (Morel et al. 2007) to the productive upwelling system of Chile. Using data from stations across a large geographic scale and range of phytoplankton concentrations, the questions addressed were: 1) Is diversity related to resource level? 2) Are taxonomic and morphological diversity linked across large scales and species pools? 3) Is resource (phytoplankton) size-structure related to tintinnid community structure under low resource conditions? The questions were addressed by estimating diversity metrics of tintinnid communities, defined as sets of species occurring in a particular place and time (Fauth et al., 1996), both taxonomic and morphological at each of the 22 stations sampled. Phytoplankton concentrations and composition were estimated using pigment analysis. Species abundance plots were constructed and compared to modeled distributions representing distinct patterns of species assemblies. The different model species abundance distributions are associated with different assumptions about the ecological equivalence of species and factors regulating the occurrence and abundance of individual species.

2 Methods

2.1 Tintinnid sampling and sample analysis

Station locations, sampling dates and depth strata sampled are given in Table 1. The cruise track is shown in Fig. 1. For tintinnids, usually 6 depths were sampled between the surface and just below the chlorophyll maximum depth (based on CTD fluorescence profiles) using a 20 l Niskin bottle. At each station, 5–10 l volumes of sample from each depth (total volumes for each station are given in Table 1) was concentrated to 20 ml by slowly and gently pouring the water through a 20 μ m mesh Nitex screen fixed to the bottom of a 10 cm dia. PCV tube. Concentrated water samples were fixed with Lugol's solution (2% final conc.). Aliquots (2–10 ml) of concentrated sample were settled in sedimentation chambers and subsequently, the entire surface of the chamber was examined using an inverted microscope at 200 \times total magnification. All material

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from all the samples was examined.

Tintinnid identifications were made based on lorica morphology and following Kofoed and Campbell (1929, 1939), Hada (1938) and Marshall (1969). Species of certain genera are known different lorica morphologies (e.g., Gold and Morales, 1976; Davis, 1981; Laval-Peuto, 1983; Wasik, 1988; Williams et al., 1994). However, only a few of the 149 species encountered in this study appeared variable and may or may not represent single species (*Tintinnopsis rapa-parva*, *Favella* spp., *Climacocylis* spp). We adopted a conservative approach, pooling apparent varieties. Empty lorica were not enumerated. For each station, data from all samples were pooled. Average cell concentrations were calculated from total counts divided by total original water sample volumes. Concentrations in terms of carbon were estimated by 1) calculating lorica volumes for each species based on combinations of geometric forms (cylinder, cone, hemisphere), 2) converting lorica volume to carbon units using the empirical conversion factor 0.05 pg C per μm^3 of lorica volume reported by Verity and Langdon (1984).

2.2 Tintinnid diversity metrics

Taxonomic diversity was estimated for each sample as the Shannon index (ln- based, e.g., Magurran, 2004) and species richness. Morphological diversity was estimated by placing species into size-classes of lorica oral diameter (LOD). Each species was assigned the average dimensions reported in Kofoed and Campbell (1929, 1939), Campbell (1942) and Marshall (1969). LOD is considered the most conservative characteristic of tintinnid loricas (Laval-Peuto and Brownlee, 1986). Size-class diameters were binned over 4 μm intervals beginning with the overall smallest diameter (12 μm) and continuing to the largest diameter encountered in a given sample. For each sample, morphological diversity was estimated as the number of size-classes occupied and a Shannon index of morphological diversity calculated using numbers and proportional importance of different size-classes (ln-based). Statistical relationships between diversity and concentration estimates were examined using nonparametric Spearman Rank Correlation.

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2.3 Tintinnid rank abundance curves

We constructed log-rank abundance curves for the tintinnid assemblages of each station by calculating relative abundance for each species and ranking species from highest to lowest and plotting $\ln(\text{relative abundance})$ vs. rank. Then, for each assemblage, we constructed hypothetical log-rank abundance curves that could fit the data by using parameters of the particular assemblage. We constructed curves for three different models of community organization: geometric series, log-series, and log-normal.

A geometric series distribution represents the result of the priority exploitation of resources by species arriving sequentially in a community (Whittaker, 1972), and is modeled by assuming that each species' abundance is proportional to a fixed proportion p of remaining resources. Thus the relative abundance of the i -th species is $(1-p)p^{i-1}$. For the tintinnid samples we used the relative abundance of the most abundant species to estimate p .

A log-series distribution represents the result of random dispersal from a larger community, such as a metacommunity in Hubbell's neutral theory (Hubbell, 2001). In a community exhibiting a log-series distribution, species having abundance n occur with frequency $\alpha x^n/n$, where x is a fitted parameter and α is Fisher's alpha, a measure of species diversity that is independent of total community abundance. For a given community with N total individuals and S species, x can be found (Magurran, 2004) by iteratively solving the following equation for x : $S/N = -\ln(1-x)(1-x)/x$ and then finding Fisher's alpha as $\alpha = N(1-x)/x$. For the tintinnid assemblages, we simply used the observed S and N for each sample to calculate x and α .

A log-normal species abundance distribution is thought to result from either a large number of species of independent population dynamics with randomly varying (in either space or time) exponential growth, such that $N(i) \propto e^{r_i}$ where r_i is a random variable. Since $N(i)$ is a function of an exponential variable, $\ln(N(i))$ should be normally distributed (May, 1975). Alternatively, species in a community that are limited by multiple factors that act on population size in a multiplicative fashion should also exhibit a

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lognormal distribution of abundances. We calculated the expected lognormal species abundance distribution for each tintinnid sample by calculating the mean and standard deviation of $\ln(\text{abundance})$ and generating three expected abundance distributions for the S species in the sample using the lognormal distribution macro program

5 in an Excel[®] spreadsheet. We then calculated the mean abundance for each species, ranked from highest to lowest, and then calculated relative abundance.

For each station assemblage, the observed rank abundance distribution was compared to these three hypothetical models using a Bayesian approach: an Akaike Goodness of fit test (Burnham and Anderson, 2002). In this test, an Akaike Information Criterion (AIC) was determined as the natural logarithm of the mean (sum divided by S) of squared deviations between observed and predicted \ln (relative abundance) for all ranked S species plus an additional term to correct for the number of estimated parameters, k (1 for geometric series and 2 each for logseries and lognormal distributions): $(S+k)/(S-k-2)$. The lower the calculated AIC value, the better the fit. A difference of 1 in
15 AIC corresponds roughly to a three-fold difference in fit, so this test statistic is sensitive enough for our data to judge the fit of the three different models.

2.4 Phytoplankton pigment sampling and analysis

Seawater samples from 10 depths at each station (except SE3 for which no samples were taken) were collected from the 12 L Niskin bottles of the rosette sampler. Volumes between 5.6 and 1 L (depending on the trophic conditions) were filtered onto
20 25 mm GF/F filters, and the filters stored in liquid nitrogen at -80°C until analysis on land. The samples were extracted in 3 mL methanol for a minimum of 1 h, with filter disruption by ultra-sonication. The clarified extracts were injected onto an *Agilent Technologies* 1100 series High Performance Liquid Chromatography (HPLC) system
25 equipped with a refrigerated auto sampler and a column thermostat, according to a modified version of the method described by Van Heukelem and Thomas (2001). Separation was achieved within 28 min during a gradient elution between a Tetrabutylam-

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monium acetate:Methanol mixture (30:70) and 100% methanol. The chromatographic column, a Zorbax-C8 XDB (3×150 mm) was maintained at 60°C. Chlorophyll *a*, divinyl chlorophyll *a* and derived products were detected at 667 nm and the other accessory pigments at 450 nm using a diode array detector. (Detection limits for chlorophyll *a* were 0.0001 mg m⁻³, injection precision was 0.4%). The different pigments were identified using both their retention times and absorption spectra. Quantification involved an internal standard correction (Vitamin E acetate) and a calibration with external standards provided by *DHI Water and Environment* (Denmark).

Total chlorophyll *a* (TChla) was assigned as the sum of chlorophyll *a*, divinyl chlorophyll *a* and chlorophyllide *a*. Seven diagnostic pigments (DP) were used to divide the phytoplankton population quantitatively, relative to the TChla concentration, into three main size classes: picophytoplankton, nanophytoplankton and microphytoplankton using the following 4 equations according to Uitz et al. (2006):

$$\text{Pico (mg TChla.m}^{-3}\text{)} = \text{TChla} (0.86\text{zeaxanthin} + 1.01\text{chlorophyllb} + 1.01\text{divinylchlorophyllb}) / \text{DP} \quad (1)$$

$$\text{Nano (mg TChla.m}^{-3}\text{)} = \text{TChla} (0.3519' - \text{butanoyloxyfucoxanthin} + 1.27 \text{ 19'-hexanoyloxyfucoxanthin} + 0.60 \text{ alloxanthin}) / \text{DP} \quad (2)$$

$$\text{Micro (mg TChla.m}^{-3}\text{)} = \text{TChla} (1.41 \text{ fucoxanthin} + 1.41 \text{ peridinin}) / \text{DP} \quad (3)$$

$$\text{DP} = (0.86 \text{ zeaxanthin} + 1.01 \text{ chlorophyll b} + 1.01 \text{ divinyl chlorophyll b} + 0.35 \text{ 19'-butanoyloxyfucoxanthin} + 1.27 \text{ 19'-hexanoyloxyfucoxanthin} + 0.60 \text{ alloxanthin} + 1.41 \text{ fucoxanthin} + 1.41 \text{ peridinin}) \quad (4)$$

Concentrations were integrated throughout the depth strata corresponding to that sampled for tintinnids. The size fractionated Chl. *a* concentrations (pico, nano and micro) transformed into % total chlorophyll were used to estimate an index of the size-diversity of chlorophyll (Shannon index, ln-based). Statistical relationships were examined using nonparametric Spearman Rank Correlation.

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3 Results

3.1 Concentrations across the transect

Tintinnid and phytoplankton concentrations co-varied (Fig. 2). Average tintinnid concentrations ranged from about 2–42 cells l⁻¹ and 4–216 ng C l⁻¹ (Table 2). Concentrations of chlorophyll varied over a narrower range of about 0.8–1.7 µg chl a l⁻¹. Phytoplankton, based on pigment concentrations (Table 3), appeared to be about equally divided between pico-sized taxa and nano-sized taxa, with a minor contribution of micro-sized taxa at all stations except for the Marquise Island (MAR1) and upwelling stations (UPW, UPX).

3.2 Relationships among tintinnid diversity metrics and phytoplankton pigment parameters

Each of the tintinnid diversity metrics employed, taxonomic or morphological, were correlated with at least one other metric (Table 4). For example, species richness was high at all stations ranging from 19 to 40 species and correlated with the number lorica size-classes and the Shannon index H'. Values of Fisher's alpha were correlated with those of H' as well as the diversity of LOD (oral size classes). However, there were few relationships among tintinnid diversity metrics and phytoplankton parameters (Table 5). Tintinnid taxonomic diversity as H' or Fisher's alpha was positively related to the depth of the chlorophyll maximum (Fig. 3). Fisher's alpha was also negatively related to average chlorophyll concentration and tintinnid concentration. The depth of the chlorophyll maximum layer was negatively related to average chlorophyll concentration (Table 3 and Fig. 4). Overall, tintinnid diversity appeared to be negatively related to resource availability as chlorophyll a and positively related to resource dispersion, in the form of the depth of the chlorophyll maximum layer.

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3.3 Rank abundance distributions

Results of the analyses of species abundance distributions are summarized in Table 6 and examples of observed and modeled distributions shown in Fig. 5. There was no obvious relationship between the type of rank abundance distribution and phytoplankton or tintinnid concentrations. The geometric series, describing a sequential monopolization of resources, described well only one tintinnid assemblage, that of St 17 which was highly dominated by a single species. The log-series, resembling that predicted by Hubbell’s neutral theory (Hubbell, 2001), provided the best match to the observed pattern in 17 of the 21 stations. The log-normal distribution, thought to result from complex species interactions, provided the best fit for 3 of the stations.

4 Discussion

In agreement with reports from survey campaigns (Kofoid and Campbell, 1929, 1939; Campbell, 1949) we found the tintinnid assemblages of the SE Pacific to be very species rich. Compared to recent geographic survey of other areas, we recorded 149 species compared to a total of 87 tintinnid species found along a transect from 42° N to 42° S from Italy through the Indian Ocean to New Zealand (Modigh et al., 2003), or the 70–80 species recorded from west to east Mediterranean transects (Dolan et al., 1999, 2002). We recorded about 30 species per location and this taxonomic diversity was paired with morphological diversity. Chlorophyll concentrations were quite low and the phytoplankton was dominated by small cells, except for stations those in or near the upwelling zone (Table 3), consistent with expectations from similar areas of the Pacific (Mackey et al., 2002).

The relationships of diversity of these micrograzers and resources were similar to those found examining trends across the Mediterranean in the late spring/early summer (Dolan, 2002). Total abundance of tintinnids increased with chlorophyll while diversity decreased. The depth of the chlorophyll maximum layer, inversely related to

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chlorophyll concentration, was positively related to tintinnid diversity (Dolan, 2000). In a subsequent study, based on samples taken at different stations in early fall from the Atlantic coast of Morocco to the Eastern Mediterranean, the only significant relationships found were between chlorophyll size-diversity and tintinnid diversity (Dolan et al., 2002). While in the SE Pacific average concentrations of chlorophyll encountered were of a range very similar to that reported in the Mediterrean transects, tintinnid abundances were lower by about half compared to the Mediterrean (Dolan, 2000; Dolan et al., 2002). The apparent variable relationships between tintinnid diversity and resources as chlorophyll led us to examine the patterns of species assembly using rank abundance distributions. The different patterns of rank abundance we examined as possibilities (geometric, log-series and log-normal) are thought to reflect different mechanisms governing the assemblage of individual communities. The distinct distributions thus reflect different assumptions concerning the ecological equivalence of species and factors regulating the abundance of individual species. Our goal was to determine which pattern dominated and if species abundance pattern was variable.

The geometric series represents a community in which dominant species limit the occurrence of rare species (e.g., May, 1975). The most abundant species monopolizes, in proportion to its abundance, part of the limiting resource; the second ranked species, in proportion to its abundance, monopolizes a part of the remaining resource, and so on, to the least abundant species. All resources are exploited and the total number of species is then largely controlled by the degree of dominance exerted by the most abundant species. The geometric pattern is found, for example, in the early successional stages among terrestrial plant communities or in relatively extreme environments (e.g. Whittaker, 1972).

A log-normal distribution represents a community in which populations are subjected to random variations or are affected by several interacting factors. It is thought to result from either a large number of species of independent population dynamics with randomly varying exponential growth, in either space or time (e.g., Huisman and Weissing, 1999). Alternatively, species in a community that are limited by multiple factors that act

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on population size in a multiplicative fashion should also exhibit a lognormal distribution of abundances. The log-normal species abundance distribution is the most common pattern exhibited by large assemblages (Magurran, 2004).

5 The log-series distribution of species abundance is predicted from Hubbell's neutral model. Local communities are part of a metacommunity, a larger widely dispersed (in space and time) group of trophically similar forms (Hubbell, 2001). With unlimited immigration, species abundance for a given community will resemble that of the larger metacommunity and will follow a log-series distribution (Magurran, 2004). Similar to the geometric series, ecological equivalence of species is assumed but in contrast dispersal plays a determining role. Log-series distributions characterize a large variety of organisms (e.g., Hubbell, 2001; Alonso et al., 2006), including communities of marine diatoms, a group of ecologically similar organisms, but not dinoflagellates, which groups autotrophic, heterotrophic and mixotrophic species (Pueyo, 2006).

15 The tintinnid communities of the SE Pacific were not well-described by a geometric series, as this model predicted a much more rapid than observed decline in relative abundance with decreasing rank than did either log-series or log-normal models. The single exception was a community a single species represented 71% of cell numbers (Table 4). The log-series models fit the data best (lowest AIC) in 17 of 21 cases, which strongly suggests that tintinnid communities are structured by dispersal limitation and exhibit weak if any competition at other than local (perhaps <1 m) scales. The log-normal distribution fit the data best in 3 cases which were not obviously distinct in any manner from the other communities.

25 Magurran (2004) has argued that species abundance distributions are difficult to compare for samples with less than 30 species, because small samples may represent a sampling of the right-hand "tail" of a lognormal distribution and therefore not detect species from the left-hand tail that are essentially "veiled" (Preston, 1962) to the observer. However, contrary to this prediction, we found that, for communities with <30 species, the fit of the log-series distribution actually improved (AIC declined) as species richness increased. Therefore we feel confident that the strong fit of the log-series dis-

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tribution to the tintinnid data, particularly for communities with low total abundance, reflects the prevalence of mechanisms, such as neutral dispersal (Hubbell, 2001), that lead to log-series distributions. For this reason, we doubt that our results reflect partial samples of communities that are otherwise described best with a log-normal distribution.

The neutral model, due largely to its assumption of ecological equivalency among species within a community, has generated a great deal of controversy (for example see Holyoak and Loreau, 2006; McGill et al., 2006; Alonso et al., 2006). There are differences of ecological significance between tintinnid species, for example LOD is related to the size of prey most efficiently grazed. However, in the SE Pacific competitive interactions may not be important simply because the food resources are insufficient or of the inappropriate size. Ritchie (1997) predicted theoretically that scarce food can lead to effective dispersal limitation rather than competition because each consumer population may not encounter all available food items within some specified time. Such a mechanism might explain why SE Pacific tintinnid communities appear to be random collections of species.

To further test whether tintinnid communities are structured by resource partitioning versus dispersal in the SE Pacific, we examined the relationship between numbers of species in a community and numbers of distinct LOD size-classes within the community and the number of species per LOD size-class. We hypothesized that if species were added to communities at random, specious communities would exhibit both more size classes as well as more species per size class. Among the communities, we found that species numbers increase with numbers of distinct size-classes present and species per size-class of LOD.

We also examined the importance of individual species characteristics in determining occurrence, by plotting occurrence rate, as % stations occupied, against lorica volume or LOD for each species and found no relationships. On the other hand, occupation rate was positively related to average abundance across all stations (Fig. 8). This last relationship is expected if occurrence of a species at a given site is dependent only on

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the large-scale population size of the species. The species with high occupation rates did not share any obvious morphological characteristics (Fig. 9). These species can be described as wide-spread, having all been found in both the Mediterrean and New Caledonia (Dolan, 2000; Dolan et al., 2006).

Overall we found strong evidence that tintinnid communities in the SE Pacific can be described by Hubbell's neutral theory. The patterns we found could be specific to the conditions we encountered. That is, a large species pool, and for most of the stations, sparse food resources. In this regard it is worth recalling that diversity increased among the stations with the depth of the chlorophyll maximum layer and decreased with the concentration of chlorophyll. High diversity was found with little food spread over a wide area coupled with low abundances of tintinnids, providing little opportunity for inter-specific relationships.

5 Conclusions

Large numbers of tintinnid taxa were found, 18–41 species per station, with a total species pool of 149. While, morphological and taxonomic diversity metrics of tintinnid communities co-varied they were not significantly related to phytoplankton diversity estimated using a pigment-based size-diversity metric. Taxonomic diversity of tintinnids, as H' or Fishers' alpha, was inversely related to chlorophyll concentration and positively to the depth of the chlorophyll maximum layer. The species abundance distributions compared to geometric, log-series and log-normal distributions showed that for most stations, the observed distribution most closely matched log-series, coherent with the neutral theory of random colonization from a large species pool. Occurrence rates of species were correlated with average abundance rather than specific characteristics of biomass or lorica oral diameter (mouth) size. Among stations, species richness was correlated with both the variety of mouth sizes (lorica oral diameters) as well as numbers of species per mouth size, also consistent with random colonization.

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Table 1. Station locations and tintinnid sampling. Cruise track shown in Fig. 1. Layer denotes depth layer sampled in meters, $n(Z)$ the number of discrete depth sampled within the layer and ΣVol the total volume (l) screened through a 20 μm mesh plankton concentrator.

| Station | Location | Date | Layer | $n(Z)$ | ΣVol |
|---------|--------------------|-------------|-------|--------|--------------------|
| SE3 | 9°56' S 142°15' W | 25 Oct 2004 | 15–70 | 2 | 10 |
| MAR1 | 8°22' S 141°15' W | 27 Oct 2004 | 15–80 | 4 | 20 |
| HLN1 | 9°00' S 136°52' W | 1 Nov 2004 | 5–140 | 6 | 30 |
| STB1 | 11°45' S 134°05' W | 3 Nov 2004 | 5–140 | 6 | 30 |
| STB2 | 13°31' S 132°08' W | 4 Nov 2004 | 5–130 | 4 | 20 |
| STB3 | 15°30' S 129°54' W | 5 Nov 2004 | 5–130 | 5 | 25 |
| STB4 | 17°13' S 127°57' W | 6 Nov 2004 | 5–210 | 6 | 30 |
| STB6 | 20°25' S 122°55' W | 8 Nov 2004 | 5–250 | 6 | 30 |
| STB8 | 23°31' S 117°51' W | 10 Nov 2004 | 5–240 | 6 | 58 |
| GYR2 | 26°01' S 114°01' W | 13 Nov 2004 | 5–270 | 6 | 60 |
| STB11 | 27°45' S 107°16' W | 20 Nov 2004 | 5–300 | 5 | 25 |
| STB12 | 28°30' S 104°16' W | 21 Nov 2004 | 5–280 | 6 | 60 |
| STB13 | 29°12' S 101°28' W | 22 Nov 2004 | 5–230 | 6 | 60 |
| STB14 | 30°01' S 98°23' W | 23 Nov 2004 | 5–230 | 6 | 56 |
| STB15 | 30°46' S 95°26' W | 24 Nov 2004 | 5–175 | 6 | 60 |
| EGY2 | 31°50' S 91°27' W | 26 Nov 2004 | 5–190 | 6 | 35 |
| STB17 | 32°23' S 86°47' W | 1 Dec 2004 | 5–175 | 6 | 55 |
| STB18 | 32°41' S 84°04' W | 2 Dec 2004 | 5–140 | 6 | 54 |
| STB20 | 33°21' S 78°06' W | 4 Dec 2004 | 5–140 | 6 | 60 |
| STB21 | 33°38' S 75°50' W | 5 Dec 2004 | 5–90 | 6 | 60 |
| UPW2 | 33°52' S 73°32' W | 7 Dec 2004 | 0–50 | 6 | 60 |
| UPX2 | 34°38' S 72°78' W | 10 Dec 2004 | 0–60 | 6 | 39 |

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Table 2. Tintinnid summary data. Data were pooled for each station. Thus, total number of tintinnids examined denoted by $\sum \text{cells}$, average concentrations of cells and carbon equivalents were calculated by dividing station sums by original sample volumes (see Table 1).

| Station | $\sum \text{cells}$ | Cells l^{-1} | ng C l^{-1} |
|---------|---------------------|-----------------------|----------------------|
| SE3 | 107 | 10.7 | 51 |
| MAR1 | 548 | 27.4 | 16 |
| HLN1 | 480 | 16 | 70 |
| STB1 | 235 | 7.8 | 29 |
| STB2 | 82 | 4.1 | 18 |
| STB3 | 105 | 4.2 | 24 |
| STB4 | 98 | 3.9 | 16 |
| STB6 | 101 | 3.5 | 4 |
| STB8 | 115 | 2.0 | 4 |
| GYR2 | 190 | 3.2 | 10 |
| STB11 | 53 | 2.1 | 4 |
| STB12 | 250 | 4.3 | 5 |
| STB13 | 324 | 5.4 | 21 |
| STB14 | 276 | 4.9 | 4 |
| STB15 | 235 | 3.9 | 13 |
| EGY2 | 354 | 6.6 | 37 |
| STB17 | 314 | 5.0 | 22 |
| STB18 | 376 | 7.0 | 158 |
| STB20 | 1670 | 28.7 | 73 |
| STB21 | 805 | 13.4 | 23 |
| UPW2 | 2540 | 42.3 | 216 |
| UPX2 | 665 | 17.1 | 50 |

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Table 3. Summary of phytoplankton pigment data. Layer denotes segment (m) of the water column sampled at 7–10 discrete depths (generally 9). CMD is the chlorophyll maximum depth (m) based on the chlorophyll vertical profile, $\sum\text{Chl a}$ is the average chlorophyll a concentration ($\mu\text{g l}^{-1}$) throughout the layer sampled. Total chlorophyll was partitioned into 3 size fractions (see methods); pChl a, nChl, μchl are, respectively, estimated average pico-sized, nano-sized and micro-size chlorophyll a concentrations ($\mu\text{g l}^{-1}$) throughout the layer sampled. All chlorophyll concentrations in $\mu\text{g l}^{-1}$. Phytoplankton samples were not taken for Station SE3.

| Station | Layer | CMD | $\sum\text{Chl a}$ | pChl | nChl | μChl |
|---------|-------|-----|--------------------|-------|-------|-----------------|
| MAR1 | 4–80 | 41 | 0.370 | 0.077 | 0.183 | 0.109 |
| HLN1 | 4–140 | 79 | 0.191 | 0.100 | 0.064 | 0.017 |
| STB1 | 4–140 | 100 | 0.165 | 0.091 | 0.059 | 0.014 |
| STB2 | 5–130 | 100 | 0.137 | 0.087 | 0.043 | 0.007 |
| STB3 | 4–120 | 120 | 0.115 | 0.076 | 0.034 | 0.006 |
| STB4 | 5–210 | 158 | 0.113 | 0.071 | 0.036 | 0.006 |
| STB6 | 5–250 | 190 | 0.076 | 0.046 | 0.026 | 0.005 |
| STB8 | 5–240 | 209 | 0.079 | 0.042 | 0.031 | 0.005 |
| GYR2 | 5–270 | 180 | 0.082 | 0.043 | 0.034 | 0.005 |
| STB11 | 5–300 | 199 | 0.080 | 0.043 | 0.031 | 0.005 |
| STB12 | 4–280 | 211 | 0.077 | 0.041 | 0.031 | 0.005 |
| STB13 | 5–230 | 160 | 0.087 | 0.043 | 0.038 | 0.005 |
| STB14 | 5–230 | 160 | 0.093 | 0.053 | 0.034 | 0.006 |
| STB15 | 5–175 | 105 | 0.139 | 0.079 | 0.050 | 0.009 |
| EGY2 | 5–190 | 80 | 0.143 | 0.073 | 0.061 | 0.009 |
| STB17 | 6–175 | 95 | 0.138 | 0.048 | 0.073 | 0.017 |
| STB18 | 4–140 | 50 | 0.153 | 0.060 | 0.074 | 0.018 |
| STB20 | 5–140 | 40 | 0.247 | 0.114 | 0.096 | 0.038 |
| STB21 | 15–90 | 51 | 0.413 | 0.106 | 0.210 | 0.097 |
| UPW2 | 3–50 | 40 | 1.697 | 0.056 | 0.138 | 1.503 |
| UPX2 | 3–60 | 3 | 0.716 | 0.324 | 0.054 | 0.377 |

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Table 4. Spearman rank correlation relationships (Rho values) among metrics of taxonomic and morphological diversity of tintinnids. For each station, estimates of taxonomic and morphological diversity were based on a pooled sample consisting of all individuals encountered in all samples from the station. Taxonomic metrics were numbers of species, the Shannon index, ln-based (H') and Fisher's alpha. Morphological metrics were numbers of lorica oral diameters (in $4\ \mu\text{m}$ size-classes) and the Shannon index of the diversity of lorica oral diameters (LOD- H'), calculated by substituting size-classes for species (see methods for details). For all pairs, $n=22$; asterisks denote significant relationships ($p=.01$). Note that measures of taxonomic diversity and morphological diversity co-vary positively.

| | # species | Taxonomic | | Morphological | |
|----------------|-----------|-----------|-----------------|---------------|----------|
| | | H' | Fishers's alpha | # LOD s-c | LOD H' |
| # species | — | 0.597* | 0.318 | 0.727* | 0.364 |
| H' | 0.527* | — | 0.704* | 0.396 | 0.550 |
| Fisher's alpha | 0.318 | 0.704* | — | 0.176 | 0.596* |
| # LOD s-c | 0.727* | 0.396 | 0.176 | — | 0.415 |
| LOD H' | 0.364 | 0.550 | 0.596* | 0.415 | — |

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Table 5. Spearman rank correlation relationships (Rho values) among metrics of the diversity of tintinnids, their concentration and characteristics of the phytoplankton. For each station, estimates of taxonomic and morphological diversity were based on a pooled sample consisting of all individuals encountered in all samples from the station. Taxonomic metrics were numbers of species, the Shannon index, ln-based (H') and Fisher's alpha. Morphological metrics were numbers of lorica oral diameters (in $4\ \mu\text{m}$ size-classes) and the Shannon index of the diversity of lorica oral diameters (LOD- H'), calculated by substituting size-classes for species (see methods for details). Concentrations represent average water column integrated values. Chlorophyll H' , the phytoplankton size diversity parameter, reflects the relative contributions of micro, nano and pico-size cells to total chlorophyll. For all pairs, $n=21$; asterisks denote significant relationships ($p=.01$). Overall, diversity appears negatively related to tintinnid and chlorophyll concentrations and positively related to the depth of the chlorophyll maximum layer which declines with chlorophyll concentration (see Table 3).

| | # species | Taxonomic | | Morphological | |
|------------------|-----------|-----------|-----------------|---------------|----------|
| | | H' | Fishers's alpha | # LOD s-c | LOD H' |
| log [tintinnids] | 0.189 | −0.195 | −0.633* | 0.250 | −0.208 |
| [chlorophyll] | 0.051 | −0.518 | −0.709* | 0.107 | −0.372 |
| chlorophyll H' | 0.071 | 0.335 | 0.386 | 0.195 | 0.320 |
| Depth Chl Max | 0.027 | 0.587* | 0.785* | −0.033 | 0.434 |

Table 6. Results of analysis of the species abundance distributions. For the tintinnid community of each station, the log-rank abundance curve was compared to model-derived geometric, log normal and log-series curves using the Akaike test. Asterisks denote the lowest AIC value indicating the closest fit.

| Station | log Normal | log Series | geometric | # spp | Dominant sp (% Σ cells) |
|---------|------------|------------|-----------|-------|---|
| MAR1 | −0.032 | −1.199* | 7.24 | 37 | <i>Steenstrupiella steenstrupii</i> (29%) |
| HLN1 | −1.29* | 0.074 | 7.68 | 35 | <i>Steenstrupiella steenstrupii</i> (22%) |
| STB1 | −1.63* | −0.603 | 8.06 | 40 | <i>Proplectella perpusilla</i> (20%) |
| STB2 | −0.22 | −1.02* | 5.30 | 19 | <i>Steenstrupiella gracilis</i> (37%) |
| STB3 | −1.72* | −1.24 | 7.23 | 31 | <i>Cantheriella pyramidata</i> (25%) |
| STB4 | −0.61 | −1.88* | 7.08 | 21 | <i>Salpingella attenuata</i> (15%) |
| STB6 | −0.36 | −1.71* | 8.89 | 22 | <i>Steenstrupiella gracilis</i> (19%) |
| STB8 | −0.48 | −2.05* | 7.50 | 27 | <i>Parundella aculeata</i> (17%) |
| GYR2 | −1.15 | −2.09* | 7.69 | 30 | <i>Cantheriella pyramidata</i> (17%) |
| STB11 | −0.74 | −1.69* | 6.76 | 19 | <i>Salpingella decurtata</i> (17%) |
| STB12 | −0.20 | −0.54* | 8.53 | 38 | <i>Salpingella decurtata</i> (12%) |
| STB13 | −1.17 | −1.17 | 8.53 | 41 | <i>Steenstrupiella steenstrupii</i> (14%) |
| STB14 | 0.63 | −1.88* | 8.00 | 36 | <i>Salpingella curta</i> (18%) |
| STB15 | −1.00 | −1.57* | 6.34 | 38 | <i>Salpingella faurei</i> (16%) |
| EGY2 | −1.33 | −2.65* | 6.42 | 38 | <i>Protohabdonella striatura</i> (14%) |
| STB17 | 1.55 | 0.66 | 0.26* | 19 | <i>Eutintinnus apertus</i> (71%) |
| STB18 | 0.83 | −1.39* | 3.12 | 23 | <i>Eutintinnus fraknoi</i> (50%) |
| STB20 | −1.54 | −2.37* | 4.59 | 29 | <i>Protohabdonella curta</i> (26%) |
| STB21 | 1.40 | −0.77* | 4.64 | 18 | <i>Protohabdonella curta</i> (31%) |
| UPW2 | −0.46 | −1.03* | 4.82 | 30 | <i>Eutintinnus tubulosa</i> (39%) |
| UPX2 | 0.69 | 0.41* | 6.15 | 32 | <i>Condenellopsis pusilla</i> (47%) |

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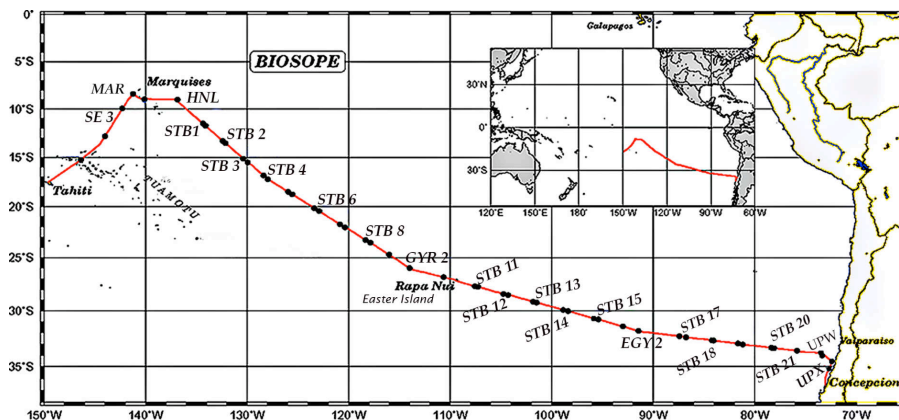


Fig. 1. BIOSOPE cruise track showing stations at which samples for tintinnid ciliates were obtained. Station locations and sampling dates are given in Table 1.

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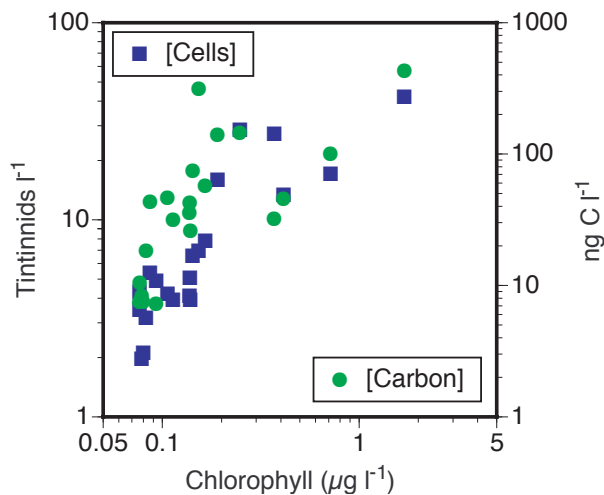


Fig. 2. Scatter plot of the relationship between phytoplankton (as chlorophyll) and tintinnid ciliate abundance among the stations. Data shown in Tables 2 and 3.

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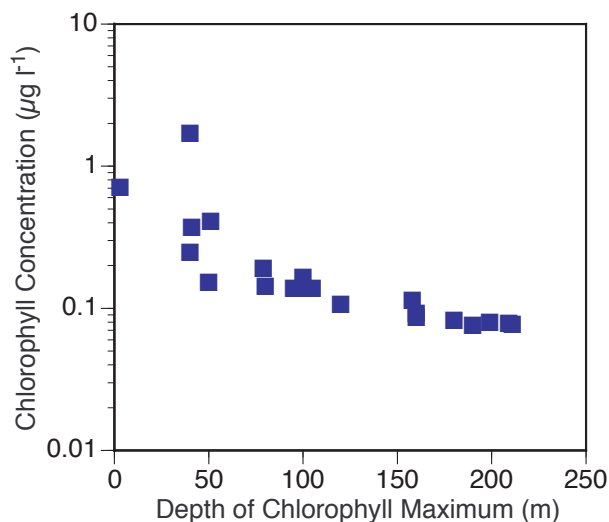


Fig. 3. Relationship between average chlorophyll concentration and the depth of the chlorophyll maximum layer among the stations sampled.

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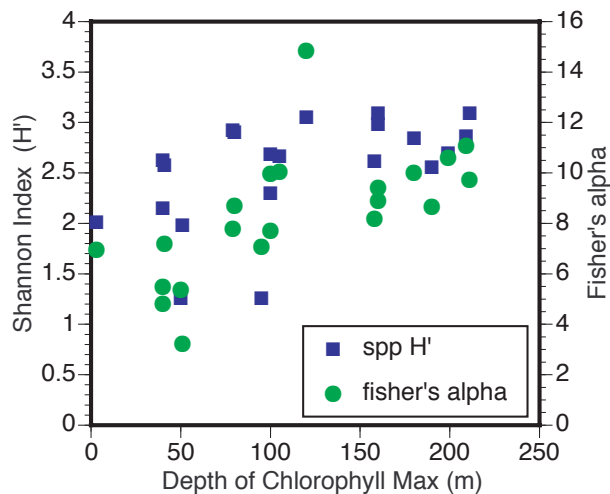


Fig. 4. Relationship between taxonomic diversity of the tintinnid community and the depth of the chlorophyll maximum layer.

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Community structure of planktonic herbivores

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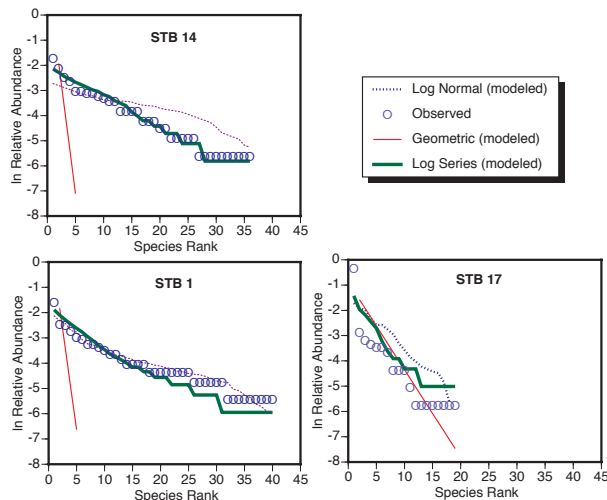


Fig. 5. Examples of species abundance distributions. Station STB 14 shows the most common pattern (15 of 21 data sets) of the log-series distribution providing the closest fit to the actual data. STB 1 was one of 3 data sets in which a log-normal distribution best matched the observed species abundance. STB 17, highly dominated by a single species (Table 4) was the only station for which the geometric distribution provided the closest fit.

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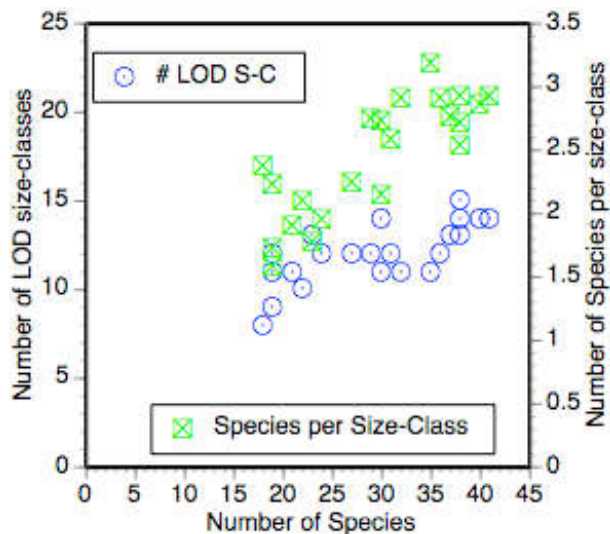


Fig. 6. Species packing in tintinnid communities across the SE Pacific Ocean. Comparing the different stations, both the number of mouth sizes, lorica oral diameter LOD in $4\text{ }\mu\text{m}$ size-class intervals, and the average number of species per mouth size increased with the number of species.

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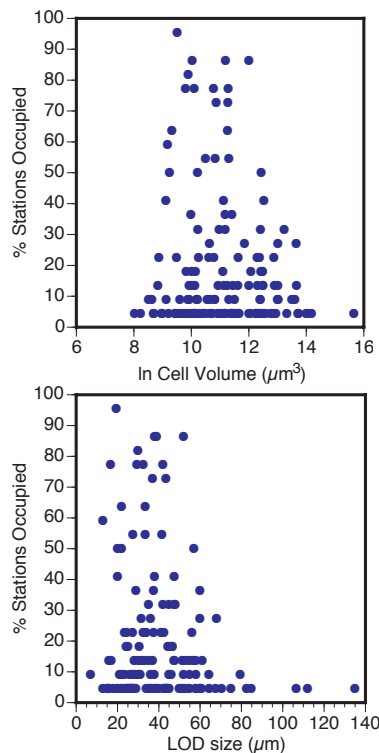


Fig. 7. Scatter plots of occurrence rates of tintinnid species, as a % of stations occupied, among the stations. The top panel shows the lack of relationship of occurrence and lorica volume and the bottom panel shows a similar lack of relation with LOD size. Neither lorica volume nor oral diameter appear linked to average occurrence.

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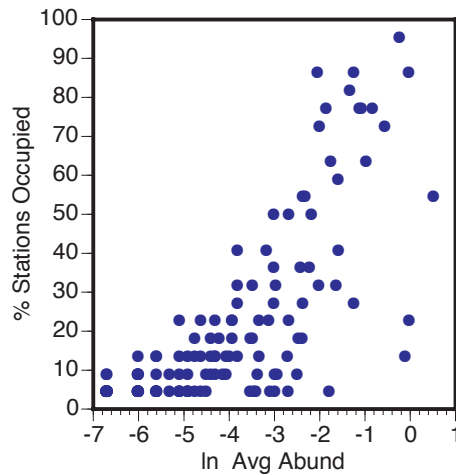


Fig. 8. Scatter plot of occurrence rate of tintinnid species, as a % of stations occupied, against average abundance across all the stations. The positive relationship between average abundance and occurrence supports the idea that overall population size determines occurrence rate.

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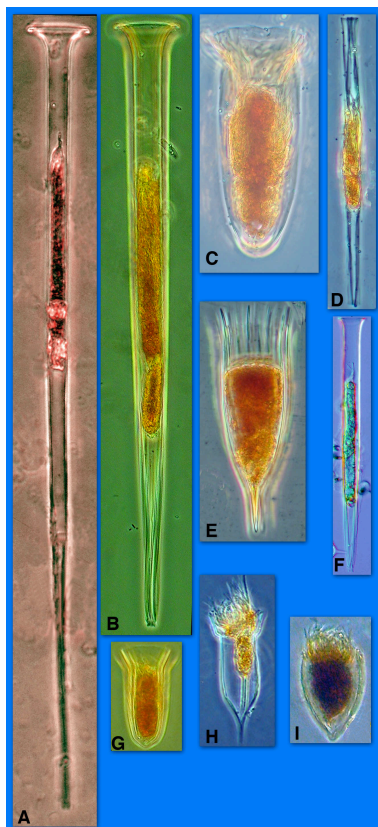


Fig. 9. Photomicrographs of tintinnid species found in over 75% of the stations sampled: *Salpingella attenuata* (A), *Salpingella acuminata* (B), *Amphorella quadrilineata* (C), *Salpingella faureii* (D), *Dadayiella ganymedes* (E), *Salpingella decurtata* (F), *Cantheriella pyrimidata* (G), *Ormsela trach* (H), *Protorhabdonella simplex* (I). The wide-spread species do not share any obvious morphological characteristics.

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